Asian Journal of Plant Sciences

ISSN 1682-3974

science alert

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Asian Journal of Plant Sciences 4 (1): 67-74, 2005
ISSN 1682-3974

Injury to Photosynthesis and Productivity from Interaction Between High Temperature and Drought During Maturation of Wheat

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Abstract: The present study aims to compare effects of high temperature and drought and to ascertain their interactions on photosynthesis and productivity of wheat. Len plants were uniformly grown in silt-loam soil [surface horizon of Ivan and Kennebec silt loams (fine-silty, mixed, mesic cumulic Hapudolls)] until anthesis and then subjected to day/night temperatures of 15/10, 25/20, or 35/30°C and moisture regimes of no drought (field capacity) and drought (-2.0 to -2.8 MPa plant water potential) in controlled environments until maturity. High temperature hastened the decline in photosynthetic rate and viable leaf area during maturation, decreased shoot and grain mass and kernel weight and soluble sugar content at maturity and reduced water use efficiency. Drought increased stomatal resistance; decreased photosynthesis, viable leaf area, shoot mass, grain mass and kernel weight and soluble sugar content and enhanced water use efficiency. Adverse effects were much more pronounced at high temperature than low temperature. Osmotic adjustment to drought was apparently promoted by low temperature of wheat to high temperature would improve its adaptation to regions with elevated temperature and either ample or deficit moisture.

Key words: Temperature, drought, interaction, grain filling, wheat (*Triticum aestivum* L.)

INTRODUCTION

High temperature and drought are major limiting factors for crops in many important production regions[1,2]. Stress is particularly detrimental to grain filling of temperate cereal species, which grow vegetatively during cool, moist conditions of spring but mature during hot, arid conditions summer. Wheat, for instance, yields nearly 14 tons ha^{-1} grain under favorable conditions, whereas average U.A. yields are only 2 to 3 tons ha^{-1}[3]. Besides limiting yields, high temperature and drought restrict plant responses to production practices and retard plant improvement by breeding[4].

Effects of high temperature and drought are usually studied individually, although the two stresses frequently occur together. Both stresses affect photosynthesis adversely, high temperature by damaging photo system II (PSII), the most labile process[5-7] and drought mostly by decreasing stomatal conductance[8,9]. Temperatures above 15°C, the optimum for wheat[10,11] also accelerate plant senescence and diminish viable leaf for photosynthesis[5,12,13]. Reduced photosynthesis is particularly detrimental during grain filling, because current assimilation provides over 80% of the yield of wheat[14].

Two wheat gain yield components, kernel number and kernel weight, are affected most by high temperature and drought stress during reproductive growth. The number of florets that produce grain is decreased by stress during anthesis and kernel weight at maturity is diminished by stress during grain filling[2,15-18]. Air temperature is the primary factor influencing the rate of grain filling[19]. High temperature speeds mobilization of assimilates for a high initial rate of grain filling; however this is more than offset by rapid senescence and greatly decreased duration[11,20]. Drought stress, in contrast, mostly decreases grain filling rate by reducing supply of assimilates and affects grain filling duration slightly[21,22].

Transpiration is an important of the energy budget that determines leaf temperature. The rate of water loss and, hence, the cooling effect by transpiration are functions of the differences in water vapor pressure between the mesophyll and the free air surrounding the leaf and of the resistance to diffusion of vapor from inside to outside the leaf[23]. Drought stress reduces transpirational cooling by affecting both the internal vapor pressure of water and the resistance to diffusion.

Differential effects of high temperature and drought on photosynthesis, senescence and grain filling and the importance of transpirational cooling suggest that the two

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Corresponding Author: Dr. Nazeer H. Shah, Wheat Botanist, Cereal Crops Research Institute, Pirsabak Nowshera, Pakistan stresses might interact. The frequently simultaneous occurrence of high temperature and drought further suggests that knowledge of their interaction is important for understanding crop responses to stress and developing improved cultivars and production practices. Objectives of the present investigations were to compare individual effects of high temperature and drought stress during the critical reproductive period of wheat and to determine their interactive effects on photosynthesis and grain filling.

MATERIALS AND METHODS

Plant culture: Spring wheat (Cv. Len) seeds were planted in 20 cm diam pots containing 5 kg of air-dried, steam-sterilized, silt-loam soil and peat moss (3:1 v/v). The soil contained 33.7, 32.5 and 360 mg kg^{-1} available N and P and exchangeable K, respectively, which were supplemented with a complete fertilizer that supplied 60, 28 and 50 kg^{-1} N, P and K, respectively. Distilled water was added as needed at 2 to 3 days intervals to maintain field capacity.

Plants were thinned to three per pot after they emerged and were grown in a greenhouse until they flowered. Temperature was set at 25/20°C day/night but varied ±2°C during the 16 h day, 8 h night. Irradiance from sunlight and high pressure sodium lamps averaged 1400 µmol m^{-2} s^{-1} PAR (400 to 700 nm), with a range of 900 to 1800 µmol m^{-2} s^{-1}, as measured with a LI-188B quantum meter (Li-Cor, Inc., Lincoln, NE) at 1200 h. Humidity was not controlled.

Spikes were tagged when anthers were extruded from florets until 50% of the tillers in each pot had flowered. The plants were then transferred to controlled environment chambers for temperature and moisture treatments one week after 50% anthesis.

Temperature and moisture treatments: Plants were randomly assigned to controlled environment chambers for treatments of 15/10, 25/20, or 35/30°C and no drought or drought. Temperature treatments were maintained during 16 h day, 8 h night periods until plants matured. Moisture conditions were continuously monitored by daily visual inspections of plants, soil moisture probe (Sav-A-Plant Tester, AMI Medical Electronics, New York, NY) observations and periodic weighing of plants and soil.

The no drought treatment, which was intended to keep the soil near field moisture capacity, was maintained by watering plants before symptoms of moisture deficiency appeared; the soil moisture probe fell below 8 units, or soil weight declined below 5.6 kg. Distilled water to bring the soil to field capacity was generally added at 5 to 8, 3 to 4 and 2 day intervals, depending on plant growth stage, at 15/10, 25/20 and 35/30°C regimes, respectively. The drought treatment to hold plant water potential in range of -2.0 to -2.8 MPa [measured with a thermocouple psychrometer (Model 74-13; J.R.D. Merrill Specialty Equipment Co., Logan, UT)] was imposed by withholding water until the lower limit was indicated by rolling of plant leaves, a soil moisture probe reading of 3 units and soil weight near 5.1 kg. Water to return the soil moisture to the upper limit was supplied every 13 to 15 d, 8 d and 5 to 7 d at 15/10, 25/20 and 35/3°C, respectively. Additions of water were recorded for all treatments.

Irradiance was 400 to 450 µmol m^{-2} s^{-1} PAR for all temperature regimes. Relative humidity, which was not regulated, ranged from 40 to 50% during light periods and 70 to 80% during dark periods.

Plant responses were determined from the day that treatments were imposed until plants reached physiological maturity. Photosynthetic rate, leaf area, plant mass and grain mass and carbohydrate content wee measured at 7 day intervals and grain filling rate, grain filling duration and water use efficiency were calculated at maturity.

Photosynthesis and stomatal resistance measurements: Photosynthetic rates and stomatal resistance of flag leaves were measured with a LI-6200 portable photosynthesis system (Li-cor, Inc.) under ambient temperature and irradiance. Readings wee initiated when CO_2 in the 0.25 L chamber reached 350 µL L^{-1} and were terminated when it declined to 320 µL L^{-1} after 30 to 60 sec. Rates were measured on three plants in each treatment of all replications.

Plant viable leaf area measurements: Leaves that were judged to be physiologically viable by lack of chlorosis or necrosis were dissected from plants used for determining the photosynthetic rates. Area of viable leaves was measured with a LI-3000/3050 meter (Li-Cor, Inc.).

Plant and grain mass measurements: Plants used for determining photosynthetic rates were cut at the soil level and spikes were detached. Vegetative parts were combined with leaves used for area measurements and dried at 70°C to constant weight for 72 h. Spikes were dried at 40°C for 72 h and threshed manually or with a head thresher (Precision Manufacturing Co., Lincoln, NE). The grain was re-dried at 40°C and the constant weight and kernel number were recorded.

Grain soluble sugar content measurements: Dried grain was ground through a 40-mesh sieve and mixed thoroughly. Soluble sugars were extracted by shaking 0.5 g samples in 20 mL of 900 L^{-1} dimethyl sulphoxide at room temperature for 1 h[24], starch was not removed from the samples by the procedure. Extracts were filtered through Whatman No.42 paper without dilution and total soluble sugar concentration was assayed with a phenolsulphuric acid reagent[25]. Total soluble sugar content was calculated as the product of concentration and grain mass per plant.

Grain filling and water use efficiency calculations: Mean grain filling rate from anthesis to physiological maturity was calculated at the average incremental change in grain mass per day during each 7 days sampling interval. The grain filling duration was calculated as the ratio of initial grain weight to mean grain filling rate[26,27]. Daily additions of water to plant containers were summed to determine total plant water use during the experimental period. Water use efficiency was calculated as the ratio of grain mass at the final sampling to the total water consumption during the experimental period.

Experimental design and data analyses: A Completely Randomized Design was used. Pots were randomly assigned to the six temperatures and drought regimes, which were replicated four times. Differences among treatment means were compared by Least Significant Differences (LSD) at the 0.05 or 0.10 probability levels.

RESULTS

Photosynthesis and stomatal resistance: Photosynthetic rates of flag leaves fell under all temperature regimes during the first week of treatment when plants were not stressed for moisture (Fig. 1). The decline was significantly slower at 15/10°C than at the higher temperatures and detectable activity persisted until the fifth week after anthesis. Rates did not differ between the two high temperatures during the first week. Plants at 25/20°C maintained detectable activity until the fourth week, whereas those at 35/30°C lost all activity by the third week.

Drought stress decreased photosynthetic rates at all temperature regimes during the first week and heartened loss of activity the following weeks (Fig. 1). Activity diminished completely one to 2 week earlier with drought than without drought at 15/10 and 25/20°C. At the highest temperatures, 35/30°C, all activity ceased after one week of treatment regardless of moisture conditions.

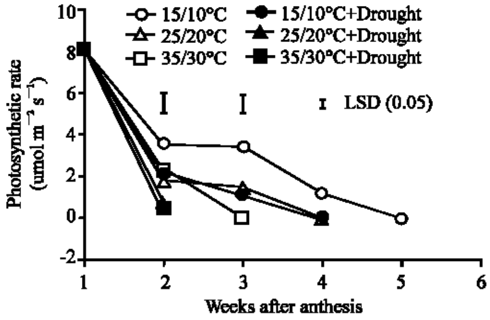

Fig. 1: Weekly photosynthetic rate of Len wheat under three temperature and two drought stress regimes during maturation

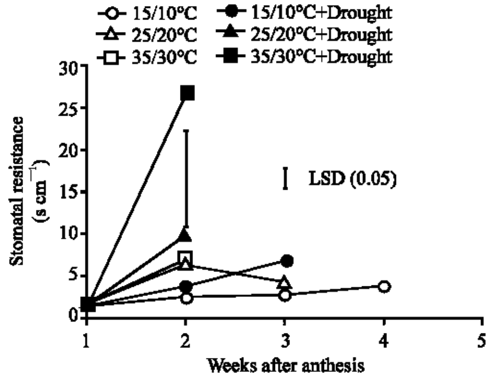

Fig. 2: Weekly stomatal resistance of Len wheat under three temperatures and two drought stress regimes during maturation

Stomatal resistance was low and unaffected by temperature in well-watered plants during the first week (Fig. 2). Resistance remained low even when photosynthetic rates declined as leaves senesced.

Withholding moisture did not change the low stomatal resistance of plants grown at 15/10°C (Fig. 2). In plants grown at higher temperature, particularly 35/30°C, however, lack of moisture caused stomatal resistance to increase rapidly during the first week.

Viable leaf area: Leaf area remained constant at the low and intermediate temperatures between the first and second weeks after anthesis when plants received adequate moisture (Fig. 3). Leaves senesced slowly at the low temperature during the following weeks, so that plants contained considerable viable leaf area for photosynthesis. Higher temperature accelerated senescence during the second week at 25/20°C and the first week at 35/30°C and little viable area for

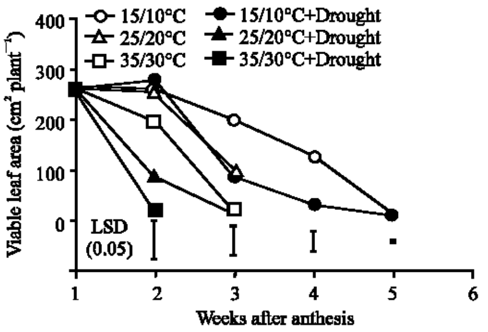

Fig. 3: Weekly viable leaf area of Len wheat under three temperature and two drought stress regimes during maturation

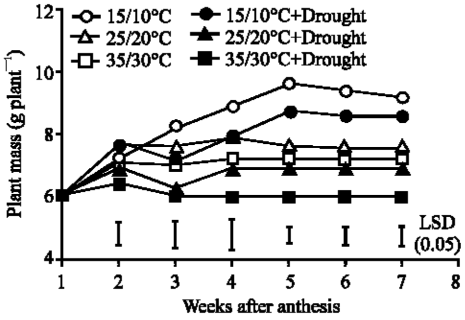

Fig. 4: Weekly total plant (shoot) mass of Len wheat under three temperature and two drought stress regimes during maturation

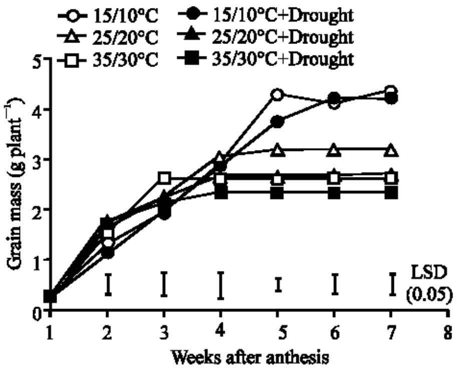

Fig. 5: Weekly grain mass of Len wheat under three temperature and two drought stress regimes during maturation

photosynthesis remained past the third week after anthesis under either regime.

Stressing plants for moisture did not affect viable leaf area at the low temperature during the first week of treatment (Fig. 3). When combined with high temperature, however, drought stress diminished leaf area rapidly. During the following weeks, lack of moisture increased senescence at the low temperature, although some viable area persisted until plants matured. Drought and high temperature together caused all leaves to senescence by the third week after anthesis.

Plant and grain mass: Total mass of shoots grew steadily for 5 weeks after anthesis in plants at 15/10°C without moisture stress (Fig. 4). Plant mass increased slightly at the other temperatures from the first week to the second week after anthesis but then became constant at both 25/20 and 35/30°C until maturity.

Drought stress had only a minor effect during the first week of treatment at 15/10°C, increasing growth slightly compared with no stress at the same temperature (Fig. 4). Mass then increased erratically until the fifth week when plants were stressed for moisture at 15/10°C. Drought stress at the two higher temperatures, particularly 35/30°C, depressed growth significantly between the second week and maturity.

Stressing plants for moisture affected the pattern of grain growth more at low temperature than at high temperature (Fig. 5). At 15/10 and 25/20°C, stress decreased grain yield mostly by depressing growth during intermediate stages. Adverse effects of drought on grain filling were less evident at the highest temperature, 35/30°C, which restricted grain growth at both moisture regimes.

Kernel weight and soluble sugar content: Changes in Kernel weight closely reflected trends in grain yield among treatments over time (Fig. 6). Kernel growth was slightly slower at 15/10°C than at higher temperatures but persisted longer, reaching a maximum of over 40 mg per kernel after 5 weeks when plants were not stressed for moisture. Like grain growth, the increase in kernel weight ended within 4 and 3 weeks after anthesis at 25/20 and 35/30°C, respectively.

Drought stress did not affect early kernel weight consistently and did not alter the duration of kernel growth (Fig. 6). Maximum weight of kernels was reduced by drought at late stages at all temperatures, however, because of slower filling at intermediate stages.

Yield components other than kernel weight remained constant among treatments and over time (data not shown). These components, tillers per plant and kernels per spike, were already established when treatments were imposed.

Accumulation of soluble sugars in grain continued for the duration of the experiment when plants were grown at 15/10°C with ample moisture (Fig. 7). The concentration in ripe grain was high, nearly 900 g^{-1}, at the low temperature (Fig. 5 and 7). Soluble sugars accumulated

Table 1: Mean grain filling rate, mean grain filling duration, plant total water use and water use efficiency of 'Len' wheat under three day/night temperature regimes and two soil moisture regimes during maturation

Regime	Grain filling rate (mg plant^{-1} d^{-1})	Grain filling duration (Days)	Plant total water use (mL plant^{-1})	Water use efficiency (G grain L^{-1})
15/10°C	0.75	47.1	1568.0	2.73
25/20°C	0.83	30.6	2223.0	1.36
35/30°C	0.88	23.3	3229.0	0.85
15/10°C+drought	0.97	25.6	976.0	4.31
25/20°C+drought	0.82	23.8	940.0	3.40
23/30°C+drought	0.79	20.7	1169.0	1.80
LSD (0.10)	0.13	3.6	258.0	1.10
CV (%)	12.3	9.8	13.4	35.90

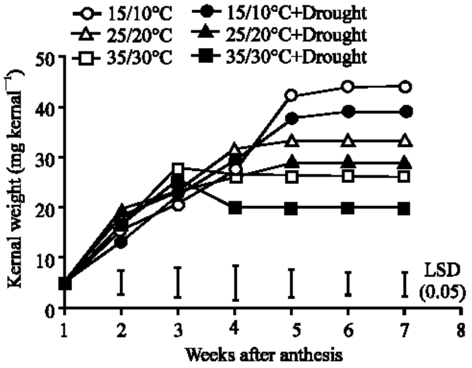

Fig. 6: Weekly kernel weight of Len wheat under three temperatures and two droughts stress regimes during maturation

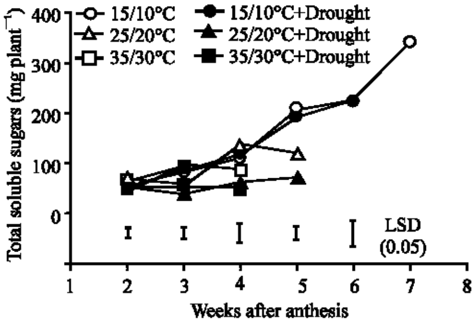

Fig. 7: Weekly soluble sugar content in grain of Len wheat under three temperatures and two drought stress regimes during maturation

slightly, but the concentration remained below 50 mg g^{-1} of final grain weight at 25/20°C. The content stayed near initial levels and the concentration in ripe grain was approximately 20 mg g^{-1} at 35/30°C. Drought stress did not affect the content or concentration of soluble sugars at 15/10°C, but it decreased the content per plant at 25/20 and 35/30°C.

Grain filling rate and duration: Grain filling rate calculated over the entire period of activity increased significantly from the lowest to the highest temperature when plants were not stressed for moisture (Table 1). Drought stress, on the other hand, did not change the grain-filling rate and prevented any response to temperature.

Duration of grain filling was longest at the low temperature without moisture stress (Table 1). Increasing the temperature to 25/20 and 35/30°C decreased the grain filling duration progressively. Stressing the plants for water likewise reduced the grain filling duration at the low and intermediate temperatures but did not shorten it significantly beyond the already brief duration at the high temperature.

Plant water use: Plant total water use rose steadily as the temperature increased when ample moisture was provided (Table 1). With-holding moisture, on the other hand, decreased total water use, as expected and eliminated the effect of increasing temperature.

Efficiency of water use for grain growth decreased from the low to the intermediate and high temperature in plants that were not stressed for moisture (Table 1). Stressing the plants increased water use efficiency at the low and intermediate temperatures but not at the high temperature. Unlike the effect on total water use, drought stress did not eliminate the decline in water use efficiency with increasing temperature.

DISCUSSION

Wheat is mostly grown in unfavorable environments the Grain Plains and Prairie Provinces of North America, The Pampas of South America, the Steppes of the USSR, North China and Australia-where yields are low[28]. Poor productivity of wheat in these regions is frequently attributed to inadequate moisture[29]. Wheat is usually not irrigated, however, because it responds poorly to supplemental moisture relative to many other species[30]. The present results demonstrate that high temperature reduces productivity of wheat, might limit the response to irrigation and interacts with drought stress to exacerbate plant injury.

The direct relationship between photosynthesis and yield suggests that a diminished supply of assimilates from the leaf source limited grain growth at high temperature[6,7]. Concurrent effects of temperature on photosynthesis and capacity of the grain sink for assimilates cannot be precluded[2,11,17,27]. High temperature does not change the maximum number and size of endosperm cells[15], however and it promotes incorporation of sucrose, the major translocation form of assimilate, into kernels[20]. The high concentration and content of soluble sugars in grains of plants at 15/10°C also indicated that photosynthetic activity produced ample assimilate and that ability of the grain to incorporate the assimilate was inadequate. Progressively lower levels of soluble sugars at 25/20 and 35/30°C, on the other hand, likely reflected the shorter supply of assimilates from reduced photosynthesis.

Drought stress decreases photosynthesis and productivity of wheat but by a different manner than high temperature. Stomata close when plants are stressed for moisture at moderate or high temperature and adverse effects are more from resistance to Co_2 exchange than from injury to plant photosynthesis[31]. High temperature, in contrast, is most damaging to PSII and has little effect on stomatal aperture when plants have ample moisture[5,32]. Reduction in viable leaf area by both stresses also probably occurs by different processes. Stomatal closure may control or initiate senescence of leaves[33], causing the viable area for photosynthesis to decrease in drought-stressed plants. Cellular constituents are degraded by proteolytic action and other activities, which are greatly accelerated by high temperature[10]. Drought undoubtedly affects the photosynthate source more than the grain sink because leaf water potential is greatly decreased, whereas spike water potential is changed little, if at all[31]. Translocation of photosynthate from the source to the sink continues at water deficit levels that inhibit photosynthesis[34].

High temperature interacted with drought stress by exacerbating most plant responses to moisture deficiency. The level of drought stress that was imposed, -2.0 to -2.8 MPa plant were potential, was moderately severe relative to values for wheat of -0.5 to -1.6 MPa in controlled environments and -1.8 to -3.5 in the field with ample moisture[31]. That level of drought stress had minor effects on plant photosynthetic rates and leaf areas, no effect on grain yield and a positive effect on water use efficiency at low temperature. High temperature accentuated injury to photosynthesis, leaf area and grain yield and negated the positive effect on water use efficiency from drought stress. This interaction is undoubtedly physiological in nature and has important practical applications.

Minimal adverse effects of drought at low temperature were probably associated with the intricate relationship among photosynthesis, osmotic adjustment and stomatal conductivity. Production of photosynthate at low temperature undoubtedly promoted osmotic adjustment to drought[35,36], causing stomatal conductivity to stay high[37] and leaf senescence to slow[33]. Water use efficiency was favored because grain growth continued and loss of moisture by evaporation and transpirational cooling was low[3,23,29]. High temperature, in contrast, aggravated plant responses to drought by injuring photosynthesis, increasing consumption of assimilates and preventing osmotic adjustment[35,36]. Initiation of senescence by stomatal closure[33] and accelerated degradation of cellular constituents by high temperature[5] accentuated loss of photosynthetic activity and leaf area. The resulting decline in grain yield, not an increase in water use, decreased water use efficiency.

Interaction of high temperature and drought stresses have applications to production and improvement of wheat. Yields are high in regions where temperature is low and moisture is ample[3] because conditions favor photosynthesis, leaf viability and long duration of grain development. Almost equally high yields are possible with low temperature and low moisture supplies, because plants can adjust osmotically and uses available water efficiently. High temperature, on the other hand, damages photosynthesis and leaf viability so grain yield are low even if precipitation is adequate for greater productivity. Regions where both stresses occur simultaneously have lowest yields because of their interaction and are unlikely to benefit substantially from irrigation because of the limiting effect of high temperature. Resistance of wheat to high temperature must be increased to improve adaptation to regions with elevated temperature and ample or deficit moisture. This would enable the crop to take advantage of favorable moisture conditions and/or adjust osmotically to low moisture conditions.

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